THE MOULTING CYCLE IN BALANUS BALANOIDES L.

D. J. CRISP AND B. S. PATEL

Marine Biology Station, Menai Bridge, Anglesey, N. Wales

Darwin, as early as 1854, noticed that a number of operculate cirripedes often moulted their skin, which included the exuviae of prosoma, appendages, penis, oesophagus, rectum and the inner lining of the mantle. He also stated that the frequency of moulting was related to the speed at which the barnacles grew.

Recently Costlow and Bookhout (1953, 1956) studied the frequency of moulting in relation to growth in recently settled cyprids of *Balanus improvisus* and *Balanus amphitrite,* but, since their observations were limited to a certain length of time after settlement, no accurate and detailed information is available regarding the seasonal fluctuations in the moulting rhythm and the factors controlling it.

The following investigation was therefore carried out to study the moulting and the factors influencing it in the boreo-arctic species *Balanus balanoides* L.

METHOD

Suitable groups of *Balanus balanoides* L. were obtained for the investigation on the shells of living *Mytilus edulis* growing on the piles of Bangor Pier in the Menai Straits, North Wales. In such a position, with a good current of water flowing past, both mussels and barnacles obtain abundant food and grow well. As soon as possible after collection all barnacles other than *B. balanoides* were removed. Usually 10–20 mature individuals were left on each shell. Care was taken not to perforate the shells of any specimens which were to be used in the experiment, since even a slight puncture, which can readily be made at the basal attachment, may lead to the death of the individual in a few days. During the first few days individuals which died were removed from the group and were not considered in the experiment.

Each group, comprising 20–30 individuals, was kept in 6-inch diameter glass crystallising dishes and the water was changed every day. It was not convenient to simulate the semi-diurnal tide; however, it was found beneficial for the barnacles to be out of water for about 8 hours each day. The dishes therefore were filled at night and emptied each morning and the cast skins present were counted. Sometimes during the breeding season pools of sperms were seen, probably indicating that copulation had occurred. Occasionally, during the period of liberation, swarms of nauplii were noted. However, if liberation occurred soon after dark, the larvae did not swarm to the side of the dish but were often devoured by the parents by the following morning. Large numbers of chocolate-red faecal pellets, containing much larval pigment and undigested chitinous appendages, were produced in consequence of this cannibalistic meal. These served to indicate that liberation had taken place. The presence of sperm pools and the evidence of liberation of nauplii were carefully noted whenever they occurred.

In some of the experiments the barnacles were fed liberally on *Artemia* larvae, and in others no food was given, a change of water being made only once a day. Both the fed and the starved animals were maintained at a series of temperatures. One series was kept in a thermostatically controlled refrigerator at $3 \pm 1°$ C., a second in a thermostatically controlled cool cabinet at 5 to $7°$ C., a third set in a cool basement, the temperature of which differed by only $1–2°$ C. from that of the mean sea water temperature, and a fourth in a laboratory where the temperature remained considerably higher, ranging between $15–21°$ C.

In order to study the influence of the parasite *Hemioniscus balani* on the moulting rhythm, infected specimens of *B. balanoides* L. and of *Elminius modestus* Darwin were collected from Brixham, S. Devon, where a high level of infection occurs (Southward and Crisp, 1954). Infected specimens of *B. amphitrite* var. *denticulata* Broch and *B. perforatus* Bruguière were collected from the warm water docks at Swansea and from the coast of the Gower Peninsula, respectively. For these experiments animals were isolated in dishes and fed on *Artemia* larvae; subsequent examination revealed whether they were infected.

Seasonal Variation in the Moulting Rhythm

Darwin (1854) in his monograph on Cirripedia mentioned that he was informed by a Mr. Peach that off the coast of Cornwall barnacle exuviae were most abundant in April–May and again in September. The specimens sent to Darwin included
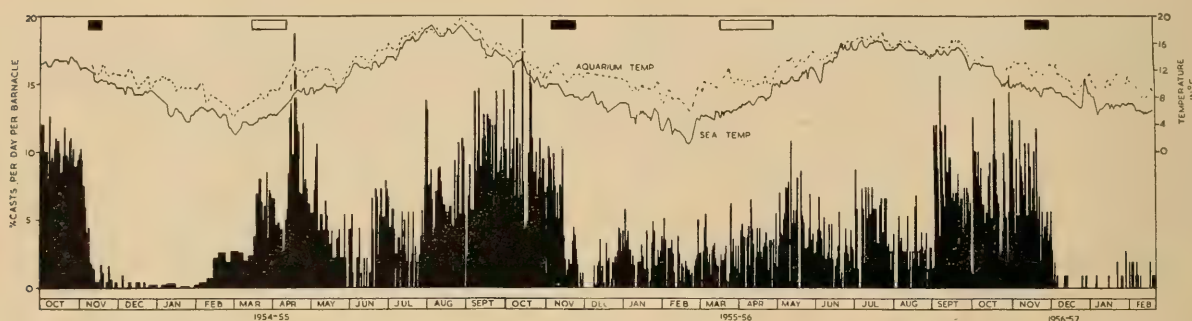

Figure 1. Seasonal variation in the moulting rhythm of groups of *B. balanoides* L. collected at approximately fortnightly intervals during the years 1954–57. Periods when fertilisation is taking place are shown by dark rectangles, and periods when liberation takes place are shown by clear rectangles.

B. balanoides L., *B. perforatus* Bruguière and *Chthamalus stellatus* Poli, but it is difficult to say to which species these exuviae belonged. Darwin also quotes Mr. Thomson's observation that 20 specimens of *B. balanoides* kept alive for 12 days shed 21 casts; presumably one must have moulted twice and the rest once. However, no information is given regarding the condition under which they were maintained.

The seasonal differences in the frequency of moulting of *B. balanoides* over a period of two successive years were determined from the moulting frequency of groups collected at short intervals, roughly once a fortnight, after which a new batch was substituted for the previous batch. It was found unnecessary to feed this species artificially, since for these short periods the moulting rate was not

appreciably influenced (see below and Table III). The moulting rates of such groups are presented in Figure 1 as per cent casts per day, together with temperatures both of the sea and of the cool basement where the groups were kept for observation.

It will be clearly seen from Figure 1 that the rate of moulting, which was about 8–12% per day in September–October, fell dramatically by November–December after the natural population had become fertilised. During December–January animals almost ceased to moult. The period of anecdysis before the animals resumed moulting varied slightly with the individual and its environment. Thereafter the moulting rate increased gradually from 3–5% per day during late February–March, to a maximum value of 8–12% per day by late April–May. However, it dropped slightly by June–August, but increased thereafter till breeding activity started.

The seasonal variation of temperature did not correspond in any way with changes in the frequency of moulting, for, though the temperature remained fairly high during summer, the frequency of moulting in both years diminished in midsummer and rose again by September and October.

Loss of Penis

Crisp and Patel (1958) reported that in *B. balanoides* only, the first cast after the period of anecdysis contained all tissues of the penis, separated by an abscission layer of new cuticle, and that this phenomenon took place whether the particular animal had been fertilised or not. Figure 2 shows the appearance of the cast skin of this species at different times of the year and the opaque appearance of the penis (Fig. 2b) in the first cast after the end of anecdysis is due to the tissues remaining in it.

During the year 1957–58 measurements of the size of the penes of from 10 to 15 cast skins were taken every day. The individuals were of the same approximate age group, mostly exceeding two years; no young individuals were used. During the period of anecdysis, measurements of penis length were made from individuals removed from the experiment. The results are shown as a series of mean values in Figure 3. A new penis gradually developed during the period of summer growth, reaching its maximum length before the onset of the next breeding season (Fig. 2a), and was subsequently lost after the period of anecdysis as described above.

Figure 4 illustrates the moulting behaviour after fertilisation had occurred and shows that all individuals gave out this particular type of cast skin once, and once only, after anecdysis; subsequent moults were normal, a stump being left in the position of the penis (Fig. 2c).

In order to confirm that the animals did not give off their penes as a result of laboratory conditions, a number of specimens were collected from the shore during the second week of January, 1957, and the penis length measured. Figure 5 shows the distribution of penis length throughout the population. The results show a clear bimodality on account of there being two types of individuals, those which had lost and those which had retained the penis. By distinguishing between those which had lost and those which had retained the penis it was possible to

FIGURE 2.   Photographs of the cast skins at different times during the year, showing the
seasonal changes in appearance of the penis.   (a) September–November: Cast with the skin
of fully developed penis.   (b) January–February: First cast after the period of anecdysis
with all tissues of the penis shed in the penis skin, rendering it opaque.   (c) March–April:
Post liberation cast with remains of egg masses, scarcely any penis present.   (d) May–August:
Summer cast with developing penis stump.

show that the loss of penes occurred earlier in barnacles growing at high water
mark than those growing at mean tide level and low water mark (Table I).   This
appeared to be due to the fact that breeding activity started first in those settled
high up on the shore (Crisp, 1959) and which were therefore correspondingly in
advance of those lower down in casting the penis.

   To investigate whether fertilisation was a necessary prelude to the loss of the
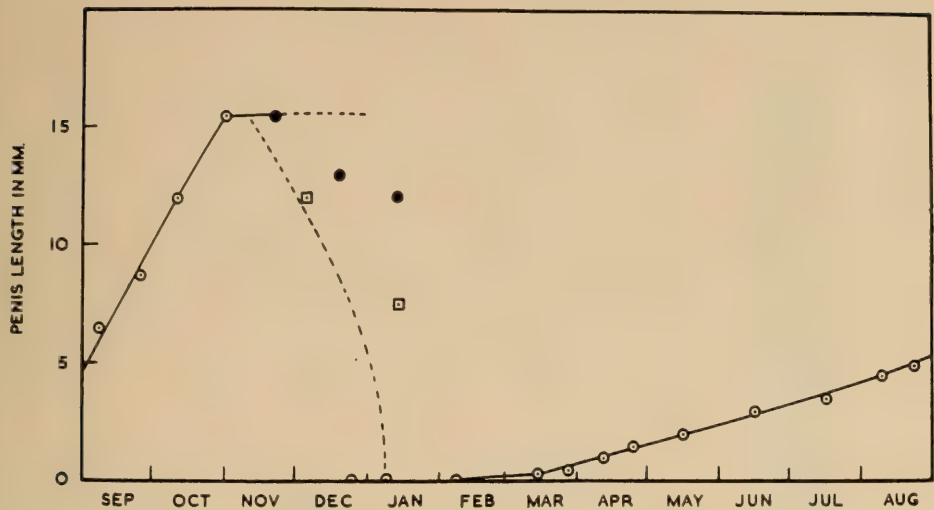
FIGURE 3. Seasonal changes in the development of the penis, measured from the cast skins. ⊡, mean values from a highly bimodal distribution of lengths due to some individuals having shed the penis. The mean size of those retaining the penis is given thus ●. Note the shrinkage in size after fertilisation, and eventual loss of the organ.

penis, mature animals collected at the end of October and early November were isolated in dishes to prevent the occurrence of copulation and fertilisation of eggs. They were maintained at temperatures corresponding closely with those in the sea. Not only the individuals which already had fertilised egg masses, but also
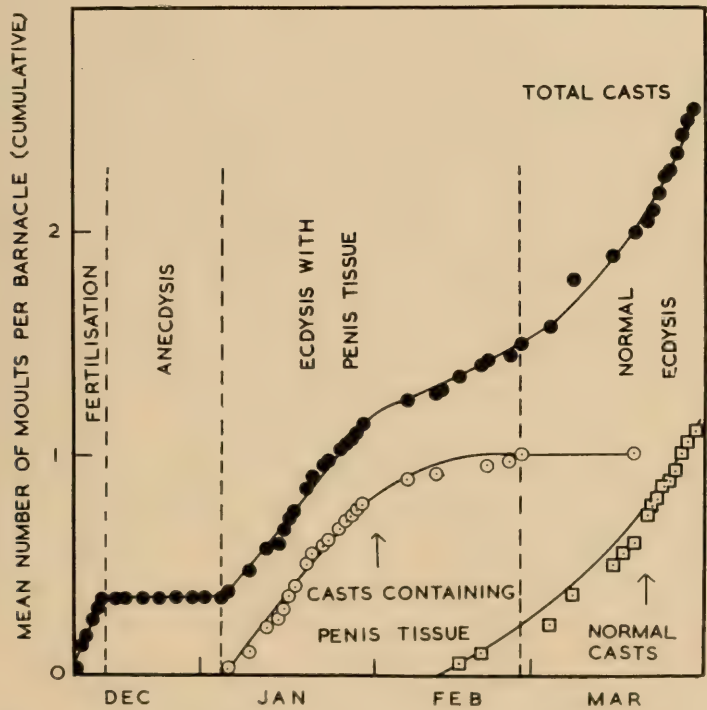

FIGURE 4. Moulting rate of 36 specimens of *B. balanoides* L. at 7° C. between 8.XII.1957 and 29.III.1958 showing how, after the period of anecdysis, the first moult contains all tissues of the penis and the subsequent moults are normal. ●, total number of all casts shed. ⊙, casts containing penis tissue, shed in January and February, one only per barnacle. ⊡, normal casts shed after the middle of February.
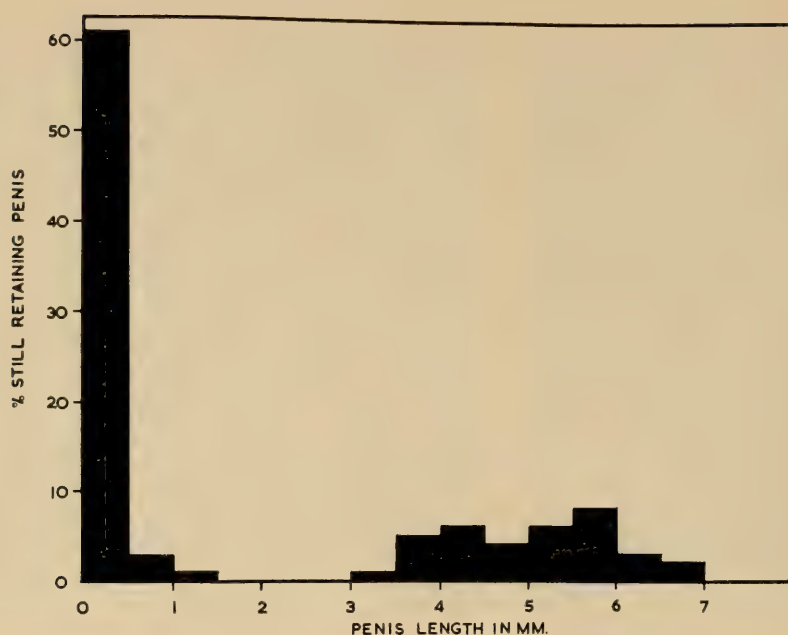
FIGURE 5. Distribution of penis lengths in a natural population of about the same year group on January 11th, 1957, showing clear bimodality on account of there being two types of individuals, those having lost and those still retaining the penis.

those which were still unfertilised gave off the cast with penis tissues (Table II). This indicates that fertilisation of itself had no marked effect on the loss of the penis.

B. balanoides could also be prevented from becoming fertilised by keeping them at fairly high temperatures (15°–21° C.) throughout the summer and autumn. These unfertilised animals continued to retain a normal penis, but if they were subsequently transferred to a temperature of 6° C. and kept cool for several weeks, they entered the breeding condition, became fertilised, and showed the typical pattern of anecdysis and loss of penis.   Others were maintained at 5° to 7° C. throughout the summer and autumn, but, on account of abnormal laboratory conditions not fully understood, reached maturity considerably later than those kept in the cool basement or those growing normally in the field.   These animals, although kept in the cold for a long period, retained a normal penis until breeding had taken place.   After having bred, all individuals gave off their penis with the first cast following anecdysis.   Furthermore, in some experiments one set of barnacles were starved and another fed; this did not influence in any way the loss of the penis.

It is clear therefore that the loss of the penis is not directly dependent on fertilisation nor on maintaining the animals at low temperature, nor on the availability of food.   It appears to be a part of a normal physiological cycle, in which the gonads as a whole undergo recession, the loss of the penis being accompanied by

TABLE I

Percentage of fertilised population, collected from different tide levels, which had still retained the penis on January 11th, 1957

Level	% with penes
H. W.	10.5
M. T.	20.4
L. W.	37.8

TABLE II

Percentage of animals which lost the penis after the period of anecdysis when maintained at 7° to 12° C.

Date animals were removed for examination	Number of specimens used		Percentage which gave off casts containing penis tissues	
	Animals without egg masses	Animals with egg masses	Animals without egg masses	Animals with egg masses
9.I.1958	188	25	42.5	28.0
11.I.1957	14	12	50.0	50.0
21.II.1958	30	36	97.0	94.0

shrivelling of the vesiculae seminalis and degeneration of testes. This takes place only after they have experienced such conditions as allow the gonads to reach their full development, and under normal circumstances for them to become fertilised.

This phenomenon was observed only in this species. Crisp (1954), however, had reported in *Balanus porcatus* (da Costa) a shortening in the length of the penis after fertilisation, followed by gradual lengthening during the summer, reaching a maximum length just before copulation.

MOULTING RATE OF YOUNG BARNACLES

Costlow and Bookhout (1953, 1956) studied the moulting rate of recently settled cyprids of *Balanus amphitrite niveus* and *B. improvisus* under varying conditions of light and food till they reached the adult stage.

During the present investigation the moulting rate of recently settled spat of *B. balanoides* was studied.
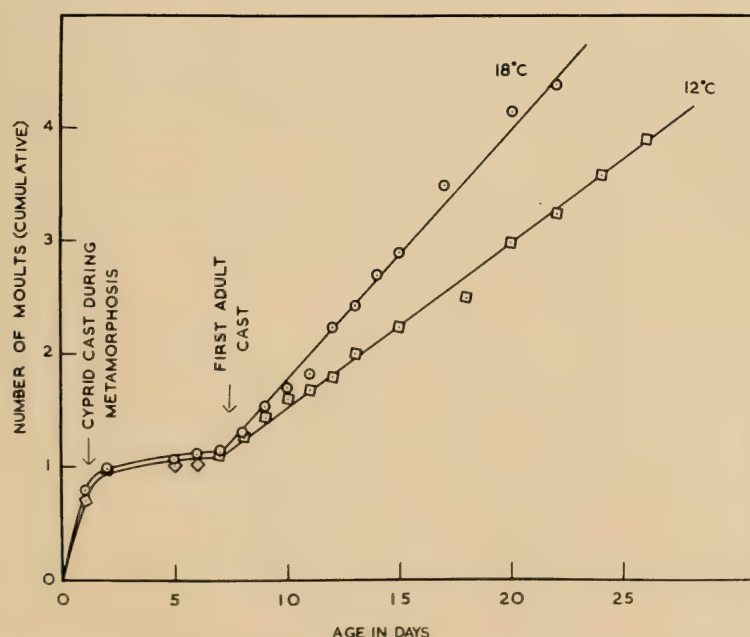

FIGURE 6. Moulting rate of young spat of *B. balanoides* L. of known age when kept at 12° C. and 18° C.

Cyprids which had settled on inert plastic plates and metamorphosed were brought into the laboratory and kept in dishes. The water in the dishes was stirred mechanically and *Chlamydomonas* sp. were offered every day as food. Since satisfactory conditions could not be guaranteed in the laboratory, these plates were returned to the sea. At the same time another batch, which had been put out for settlement, was brought into the laboratory, and was placed in a dish; the water was stirred and the animals fed as before. Several plates were thus kept in rotation between the laboratory and the sea, a few plates being kept continuously in the laboratory. The number of exuviae was recorded each day.

Figure 6, drawn from the sets of results, illustrates the cumulative number of casts shed during the first few weeks after settlement. Metamorphosis of cyprids occurred after 24 to 36 hours and the apodemes of the paired eyes, the bivalve carapace and the exuviae of the thoracic limbs were shed (Crisp and Stubbings, 1957). No further ecdysis occurred for at least 5 days. The time of the first adult cast varied considerably, but on average it took place between 9 and 10 days after metamorphosis. This was longer than the corresponding period for *B. amphitrite* (Costlow and Bookhout, 1956), in which the first cast occurred between 3 and 5 days after metamorphosis. Thereafter *B. balanoides* moulted approximately once every four days at 18° C. and about once every six days at 12° C. From Figure 6 it will be clearly seen that the moulting rate of the rapidly growing spat was at least double the maximum rate of moulting of the adult over the same period of the year (Fig. 1).

Factors Influencing Ecdysis

a. *Feeding*

Groups of *B. balanoides* were maintained at several temperatures, some being fed on *Artemia* larvae and other groups having the water changed only. Those groups which were given *Artemia* were observed to be beating the cirri intermittently throughout the day and producing dark red faeces. The starved groups, on the other hand, were active for a short time after the water in the dishes had

Table III

Moulting rate of B. balanoides under varying conditions of temperature and feeding. The animals were collected on July 1st, 1957

| Number of animals available	Condition		Rate of moulting	
	Fed or starved	Mean temperature	First 10 days after collection	First 60 days after collection
46	fed	19.5° C.	0.10 casts per day	0.13 casts per day
47	starved		0.10 casts per day	0.065 casts per day
22	fed	17.0° C.	0.12 casts per day	0.12 casts per day
21	starved		0.10 casts per day	0.06 casts per day
27	fed	6.0° C.	0.05 casts per day	0.046 casts per day
29	starved		0.05 casts per day	0.032 casts per day
27	fed	3.0° C.	0.05 casts per day	0.03 casts per day
27	starved		0.05 casts per day	0.03 casts per day
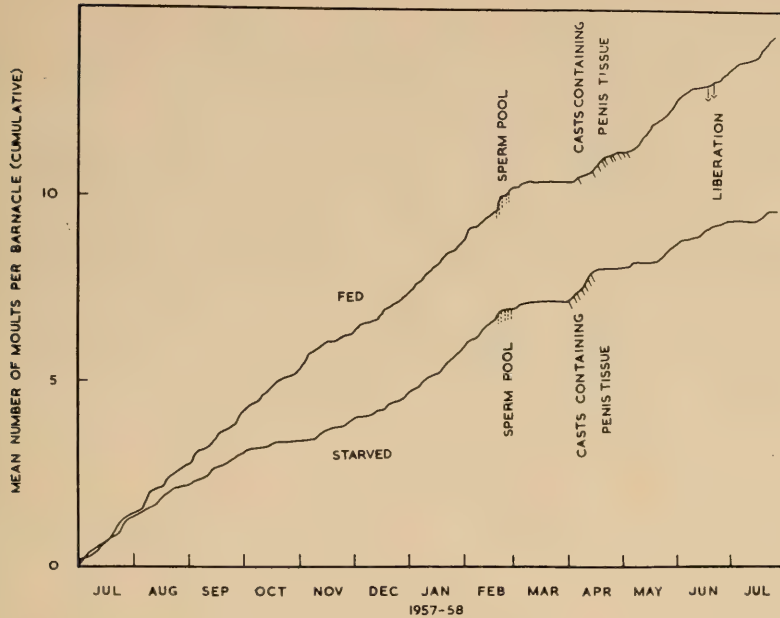
FIGURE 7. Moulting rate of groups of *B. balanoides* L. showing the effect of starvation at 5-7° C. Sperm pools indicate that fertilisation was taking place. Casts containing penis tissues are shown by oblique lines and liberation by small arrows.

been changed, but remained quiet for the rest of the day except for very occasional beating.

As can be seen from Table III, both fed and starved batches moulted at approximately the same frequency immediately after collection and for the following ten days. Thereafter the fed barnacles continued to moult at the same or at a slightly decreased rate, but the starved barnacles showed a progressive reduction in frequency but did not cease to moult altogether. These long-term changes are shown in Figure 7 for animals kept at 5 to 7° C. It will be noticed that after anecdysis the moulting rate was low, but it recovered much more rapidly in those individuals which were fed. These results suggest that the amount of reserve food available is important in determining the moulting rate. The results in Table III show that at higher temperatures there is an even more marked difference between fed and starved individuals due, no doubt, to the greater loss of reserve food at the higher metabolic rate.

b. *Temperature*

Southward (1955a), who studied the influence of temperature on the cirral activity of *B. balanoides,* reported that the rate of cirral beats increased linearly with the increase in temperature from 3 to 20° C. The rate of beating, however, fell with a further rise in temperature, 31 to 32° C. being lethal.

Similarly (Fig. 7) the moulting rate of barnacles fed on *Artemia* increased linearly with the rise in temperature from 3 to 20° C. The moulting rate of starved specimens, on the other hand, increased from 3 only up to 12° C. and then diminished with a further rise in temperature. If, as seems likely, the rate of moulting is influenced by the food reserves available, it would not be surprising that with increased metabolic rate at higher temperatures the reserves would fall

sufficiently to reduce the moulting rate. After a sufficient period the effect of loss of reserves might more than counteract the normal increase in moulting rate with temperatures, so that the moulting rate actually fell with rise in temperature.

Both fed and starved specimens moulted at the same frequency at the lowest temperature (Table III, Fig. 8) ; the reason for this might be the fact that at 3–4° C. those which were offered food remained quiet and fed very little, while those which were starved did not lose reserve metabolites at any appreciable rate at low temperatures.

Southward kept his specimens only for a very short time at 25 to 30° C. and was able to measure their cirral beat at these temperatures; however, both fed and
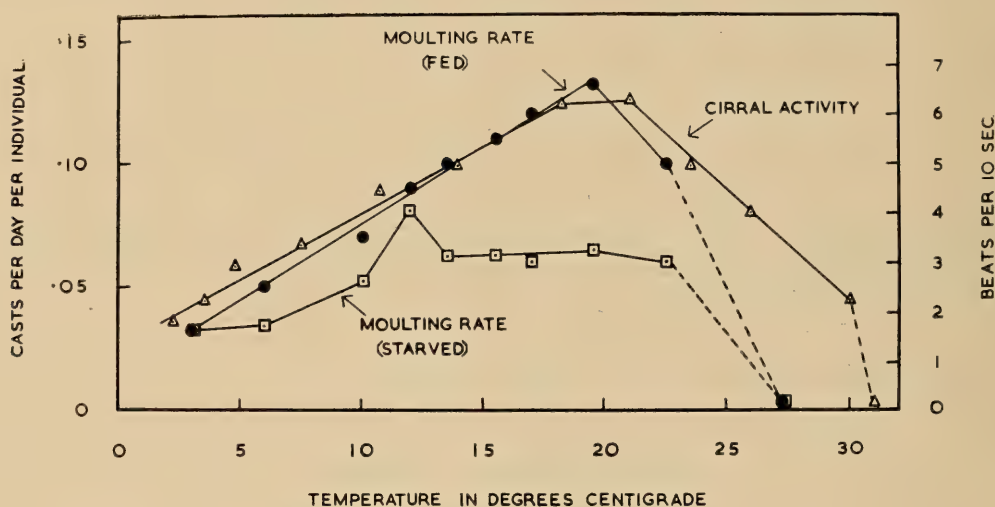

FIGURE 8. The effect of temperature and feeding on the moulting rhythm of *B. balanoides* L. and the effect of temperatures on cirral activity (from Southward, 1955a).

starved specimens during the present series of experiments died if kept for more than three days at 25 to 27° C.

c. *Breeding*

The majority of recently fertilised animals abruptly ceased to moult for some six to eight weeks (Fig. 9) ; this might be regarded as an adaptation to prevent recently oviposited eggs, which are not yet hardened, from being shed with a cast. However, after anecdysis, the still gravid barnacles resumed moulting, especially if they were fed (see Figure 7) and were found to have cast the skin with a torn-off mantle lining, due to the pressure exerted by the egg masses. The latter had by this time become hard and were pressed well up against the mantle lining of the parietes and basis. Occasionally only the exuviae of the appendages and prosoma were shed, the mantle lining being retained and shed later at the time of the liberation of the nauplii hatched out from the egg masses.

It will be seen from Figure 9 that the barnacles which were kept from being fertilised by being artificially isolated continued to moult when the fertilised population had ceased. Nevertheless they showed a sharp fall in moulting rate by the end of November. This suggests that the drop in the moulting rate may be due to a basic physiological rhythm, like that controlling the loss of the penis and

degeneration of the gonads, and that the sudden onset of this process in fertilised barnacles may be due to the stimulus of copulation or oviposition.

d. Effect of emersion on moulting

As Darwin (1851) observed, the skin cannot be shed except when the barnacle is immersed in water. The period of emersion of organisms which grow between low water neap and high water neap tide levels never exceeds about 12 hours. In a humid environment intertidal barnacles may be kept out of water quite healthily
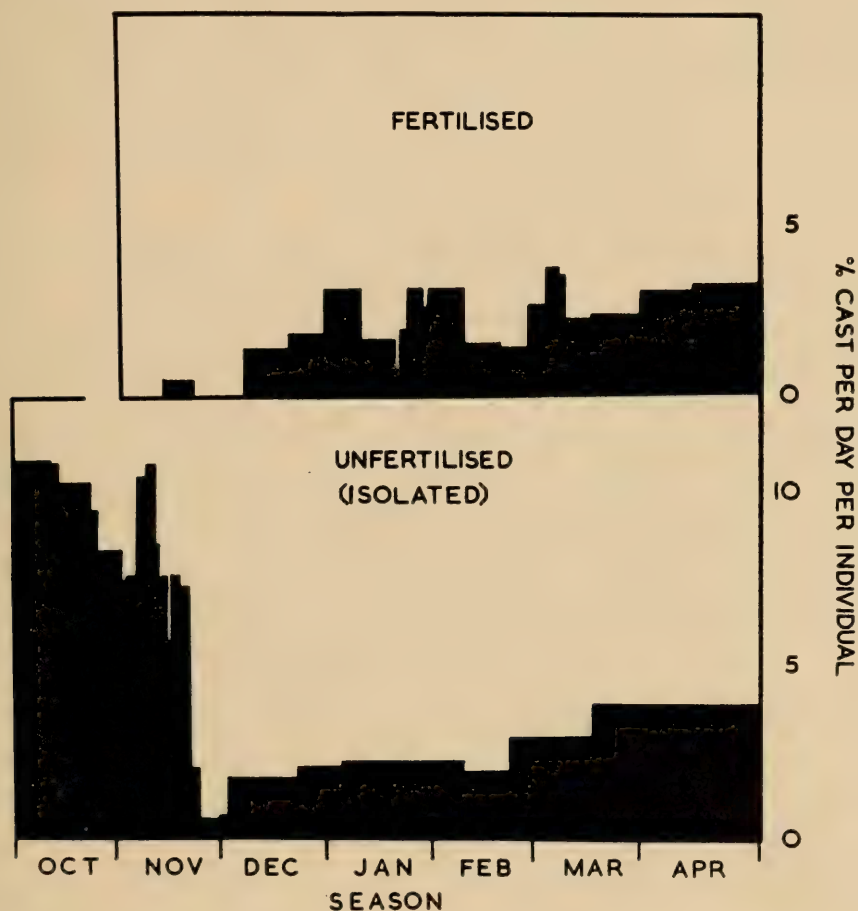

FIGURE 9. Moulting rate of isolated specimens not carrying embryos and of those with fertilised egg masses, measured over the same period. Fertilised specimens show an immediate drop to zero; unfertilised specimens continue to moult freely in mid-November, but show a fall in late November at the end of the normal breeding season.

for several days. It is thus possible to ascertain whether the frequency of moulting is influenced by an abnormally long period of emersion.

Four groups of barnacles growing under nearly identical conditions on settlement plates on a raft were brought into the laboratory. Here they were kept under a damp cloth for varying periods of time. The total number of casts shed when the barnacles were introduced for a period of 24 hours into aerated sea water was recorded. In Table IV the aggregate percentage of casts (per 100 barnacles) is shown against the total number of days kept in the laboratory. The letter "D"

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TABLE IV

*Moulting rate in relation to the treatment of various groups of barnacles; letter "D"
indicates the days when the specimens were kept dry, on the other days
they were kept in sea water at 12° C.*

(1)	(2)	(3)	(4)	(5)	(6)	(7)
Group	Number of barnacles used in experiment	1st day	2nd day	3rd day	4th day	Total casts after 4th day
a	382	D	D	D	26.2%	100
b	373	D	D	22.0%	35.4%	132
c	370	D	14.3%	20.2%	28.6%	106
d	453	3.7%	D	D	33.1%	150
Mean	—	—	—	—	30.9%	(7.7 ∞ per day)

$\chi^2 = 9.98$

indicates the days when the groups were kept dry, and no casts were therefore emitted. Column 7 gives the total number of casts for the whole period.

It is clear that moulting proceeds steadily throughout the experiment and is not delayed significantly as a result of the barnacle being out of water. The numbers of casts found after 4 days in the different groups, a, b, c and d, which were treated differently give a value for χ^2 of 9.98 when compared with the expectation of 7.7% per day per individual. This is slightly higher than the value of $\chi^2 = 7.8$ for the 5.0% significance level. Since, however, there was no consistent trend in the moulting rate in relation to the emersion period, the significance of the χ^2 value was probably due to intrinsic variations in the rate of casting of the four groups, a, b, c and d; such variations are frequently observed between groups of individuals from apparently similar habitats. The data of Table IV, rearranged to show the moulting rate in relation to the time kept out of water, are displayed in Table V. The rates of casting are closely uniform and the χ^2 test applied to the differences was found not to be significant ($\chi^2 = 6.26$ for 3 degrees of freedom). The number of casts produced in a given time is therefore not altered significantly by emersion up to a period of four days.

TABLE V

Moulting rate in relation to the total time out of water

(1)	(2)	(3)	(4)
Number of days out of water	Barnacle days (No. of barnacles × no. of days)	Number of casts	Moulting rate (% casts per day)
4	1528	100	6.55%
3	2478	215	8.69%
2	740	53	7.17%
1	1566	120	7.68%

$\chi^2 = 6.26$

It was often noticed that the rate of moulting for the first day or two was higher than the average for the whole period. This may have been partly due to the individuals having been out of water since the previous high tide. Possibly also the changed conditions in the laboratory caused a temporary rise in the rate of moulting. However, this small initial rise had no significant influence on the average rate taken over two or three weeks.

e. Tidal periodicity

In many marine organisms, especially in lamellibranchs and in annelids, the effect of moon and tide on the breeding cycle had been well established (Korringa, 1947.) However, Crisp and Davies (1955) reported that *Elminius modestus* bred at any time irrespective of the tidal cycle.
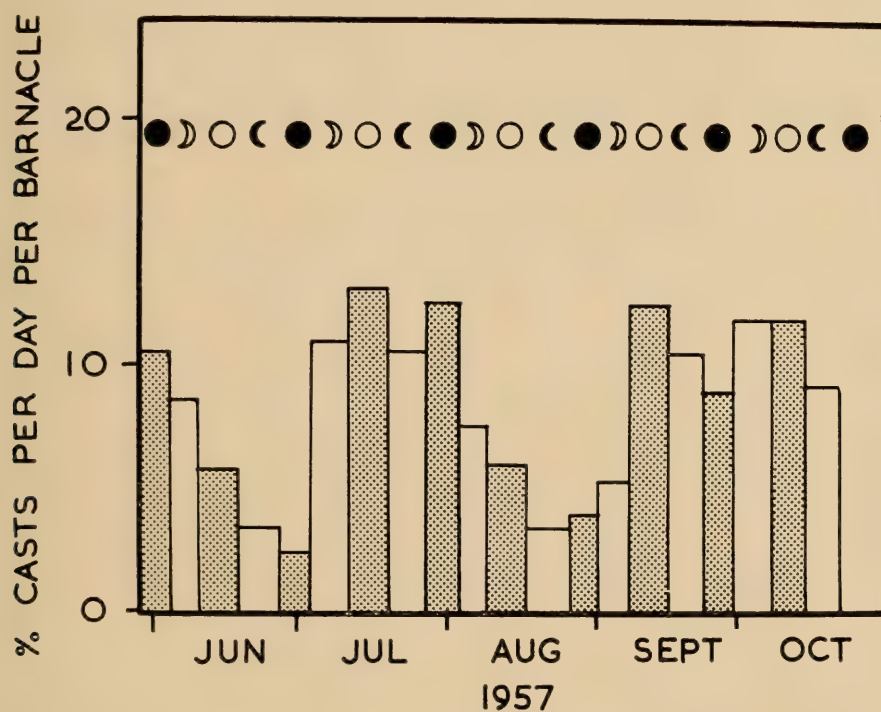

FIGURE 10. Average moulting rate of the groups of *B. balanoides* L. collected at monthly intervals and kept at sea temperature over the spring and neap tide periods (shown by moon phases). Stippled blocks, average moulting rate over the spring tide period; clear blocks, average moulting rate over the neap tide periods.

Churchill (1917–18) studied the effect of the lunar cycle on the moulting rhythm of the blue crab *Callinectes sapidus*, but on the basis of his results dismissed the popular belief prevailing that both moon and tide had a marked effect on the moulting of crabs as being a folklore superstition. However, Wheeler (1937) in *Anchistioides*, Nouvel and Nouvel (1939) in the mysid *Praunus flexuosus* and Nouvel (1945) in *Leander serratus* found that the largest numbers of exuviae were shed on the day corresponding to the largest tide. However, their observations were made only over a single lunar period and may therefore be fortuitous. Kinne (1953, 1959) found no tidal rhythm in the moulting of the amphipod *Gammarus duebeni*. Tidal rhythm in moulting does not therefore seem to be of general occurrence in the Crustacea.

During the present investigation experiments were carried out to test if any tidal rhythm could be found in barnacles. Each tidal cycle was divided into two periods, approximately midway between the largest and the smallest tides, one period corresponding to the spring and the other to the neap tides (shown by moon phases in Figure 10). The average moulting rate of groups of animals collected at monthly intervals was determined for pairs of successive neap and spring periods. The difference between the average for neap and spring periods was tested by applying Student's "t" test and found to be insignificant. Ecdysis therefore occurred at approximately regular intervals, provided barnacles were immersed, irrespective of the tidal cycle.

f. *Effect of tidal level*

Animals were collected from three different tidal levels and their moulting rate for the first ten days was recorded. It can be seen from Table VI that there was no significant difference in the moulting rhythm. Though Southward (1955b) did record specimens (*B. balanoides*) collected from low water mark beating

TABLE VI

Moulting rate of B. balanoides, *collected from different tide levels, for first 10 days*

Dates animals were collected	Temperature	Casts per day per individual		
		H. W.	M. T.	L. W.
22nd Jan.	8–10° C.	0.03	0.04	0.05
29th Jan.	8–10° C.	0.025	0.03	0.04
28th Feb.	8–10° C.	0.06	0.04	0.04
5th Sept.	14–16° C.	0.110	0.10	0.12

markedly faster than those collected from higher up, when he repeated the experiment on the following day with the same specimens he found that the differences had disappeared. Neither moulting nor cirral activity appears to be influenced by tidal level.

g. *Influence of light on moulting rhythm*

It has been claimed that light has an inhibitory action on the moulting rhythm of Crustacea (Nouvel, 1945). However, Costlow and Bookhout (1956) did not find any significant differences in the moulting rate of the series of young spat of *B. amphitrite niveus* reared under different conditions of illumination.

During the present series of experiments the influence of light on the moulting rhythm of adult barnacles was investigated. Groups of barnacles were collected from the shore and maintained under three different conditions. One batch was kept under a light-tight box kept in continuous darkness. A second batch was kept in a continuously illuminated, well ventilated box, illuminated by a 25-watt bulb. The third batch was exposed to natural variations of light conditions, 12 hours light during the day and 12 hours darkness at night. All were kept at the

same temperature of 10° C. No significant difference in moulting rate was found over a period of 50–60 days.

h. *Influence of parasite Hemioniscus balani*

The majority of the species of British barnacles was found to be capable of harbouring the isopod *Hemioniscus balani* in the mantle cavity, in the space normally occupied by the fertilised egg masses. Crisp (1954) found this parasite causing castration of the female gonads in *B. porcatus* (da Costa) and later a similar effect was reported in *Elminius modestus* (Crisp and Davies, 1955).

The effect of the parasite on the moulting rhythm was therefore investigated using infected *B. balanoides, Elminius modestus, Balanus perforatus* and *B. amphitrite* var. *denticulata*. It will be seen from Table VII that the presence of the parasite had no significant effect on the moulting cycle of the host; the intermoult periods of infected and uninfected barnacles were not significantly different. However, as with fertilised individuals which had eggs in the mantle space, the speci-

TABLE VII

Frequency of moulting of specimens infected with Hemioniscus balani *and of uninfected specimens collected from the same locality*

Species	Temperature	Number of animals used in experiment	Percentage infected with *Hemioniscus balani*	Mean intermoult period in days of	
				Individuals with *Hemioniscus*	Individuals not infected
Balanus balanoides	12° ± 2° C.	35	57%	10.9	9.0
Elminius modestus	12° ± 2° C.	10	50%	7.3	7.3
Balanus perforatus	13° ± 2° C.	20	5%	6.0	6.4
Balanus amphitrite	15° ± 2° C.	100	6%	10.3	9.8

mens harbouring the parasite were found to shed exuviae with torn-off mantle linings. On no occasion was the parasite rejected with the cast, except in the large barnacle *B. perforatus*. This species was observed to reject the parasite enclosed within the casts, and this may account for the normally very low degree of parasitism present compared with that found in other species in the same vicinity.

SUMMARY

1. The seasonal variations in the frequency of moulting of boreo-arctic species of the operculate barnacle *Balanus balanoides* L. were studied during the years 1954–57 by observing groups of barnacles kept in the laboratory at temperatures corresponding to that of sea water. The rate of moulting, which was about 8 to 12% casts per day per barnacle during October–November, fell sharply by November–December and fertilised animals underwent a period of anecdysis for about 6 to 8 weeks. They resumed moulting at a slower rate, reaching a maximum by May with a slight decrease in June–August, rising again towards the breeding season in November.

2. In this species the first cast after the period of anecdysis always contained all tissues of the penis, separated by an abscission layer of new cuticle. Neither food, temperature nor the act of fertilisation were directly responsible for the loss of the penis. The evidence indicates that the loss of the penis is part of a physiological cycle in which gonads undergo recession after they have reached full development. A new penis gradually developed during the period of summer growth, reaching its maximum length before the onset of the breeding season.

3. Feeding influenced the moulting rhythm, but the effect made itself felt only after the first 10 to 15 days following collection from the shore. The moulting rate of specimens maintained without food for a period longer than this (*i.e.*, for about 30 to 60 days) fell considerably from the initial value, but animals fed on *Artemia* larvae continued to moult at about the same rate as when freshly brought in from the shore.

4. The moulting rate of specimens given food increased linearly with the rise in temperature from 3–20° C.; on the other hand the moulting rate of starved specimens only increased from 3–12° C. and fell considerably with further rise. Temperatures higher than 25° C. were lethal to both groups.

5. Neither the lunar cycle nor the tidal level had any influence on the moulting rhythm.

6. The parasite *Hemioniscus balani,* which caused castration of the female gonads, did not influence the frequency of moulting.

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